

Colony Reproduction by Budding in the Polygyne Form of *Solenopsis invicta* (Hymenoptera: Formicidae)

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ABSTRACT Indirect evidence has suggested that polygyne colonies of the red imported fire ant, *Solenopsis invicta* Buren, reproduce by budding. To verify directly the occurrence of budding, queens in polygyne colonies were marked with fine wire and introduced to two field sites previously cleared of fire ant mounds. After 4-5 mo, all mounds were mapped and collected. Marked queens originating from the same colony were found distributed among three to eight different mounds separated by up to 50 m. Marked queens from different colonies were not recovered in the same mound, suggesting that queens do not move freely among established mounds which lack some former connection. The total weights of the colonies increased about four times during the course of the study, indicating substantial growth of colonies in addition to active budding.

KEY WORDS Insecta, fire ants, polygyny, colony reproduction

THE RED IMPORTED FIRE ANT, *Solenopsis invicta* Buren, a native of South America, occurs in two social forms within its range in the southeastern and southcentral United States. The most common form is monogyne (i.e., colonies have one inseminated functional [egg-laying] queen), whereas colonies of the polygyne form contain several to hundreds of functional queens (Glancey et al. 1973, Fletcher et al. 1980, Fletcher 1983, Lofgren & Williams 1984, Vargo & Fletcher 1987).

In addition to their distinctive social structures, the monogyne and polygyne forms of this ant differ in other important features. Electrophoretic data show that monogyne colonies consist of simple single family units, whereas polygyne colonies comprise individuals of varying degrees of genetic relatedness (Ross & Fletcher 1985). Workers of polygyne colonies are smaller (Greenberg et al. 1985), are less aggressive toward nonnestmate conspecifics (Mirenda & Vinson 1982), and are more tolerant of the presence of multiple queens (Fletcher & Blum 1983). Queens of polygyne colonies are less fecund than those of monogyne colonies (Fletcher et al. 1980, Greenberg et al. 1985, Vargo & Fletcher in press), and polygyne colonies produce fewer sexuals, presumably because of higher levels of inhibitory pheromones from the combined production of the many queens (Vargo & Fletcher 1986, 1987).

Another difference between the two social forms of *S. invicta* may lie in the mode of colony reproduction. Colonies of the monogyne form reproduce through mating flights and claustral founding, as is typical of ants (Markin et al. 1972, Tschinkel &

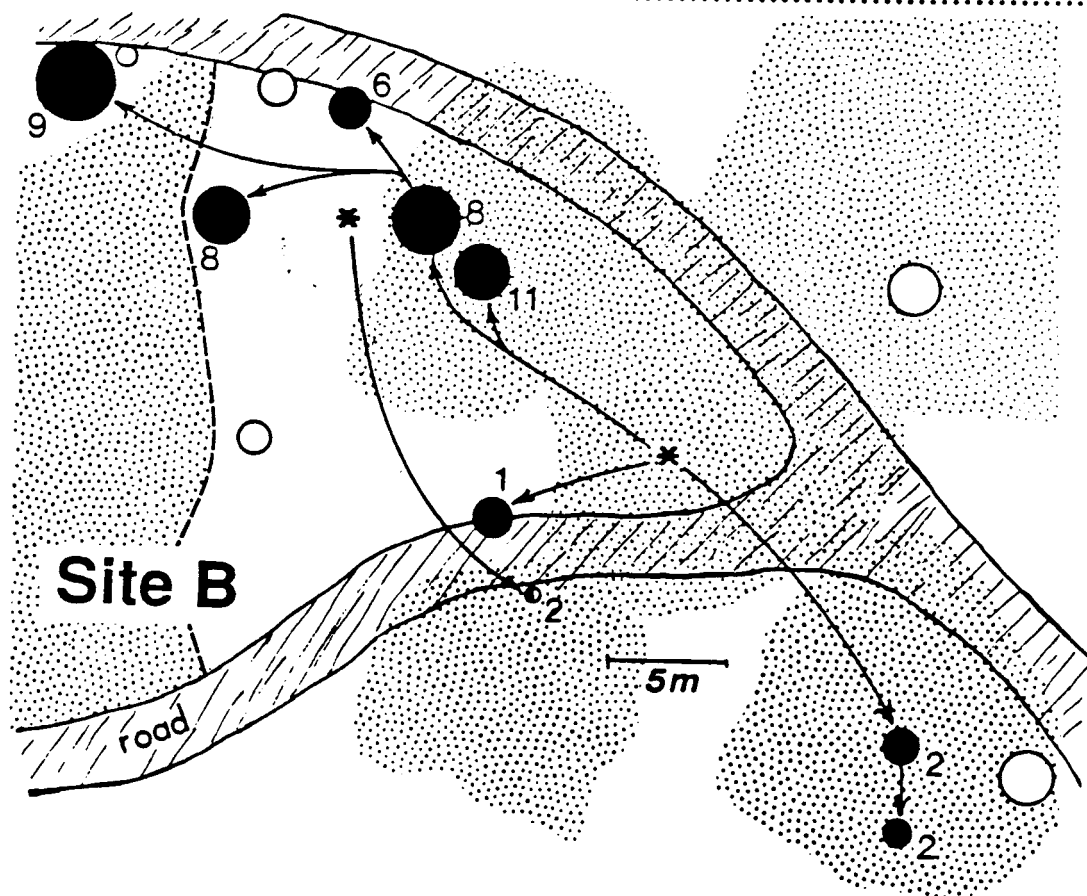
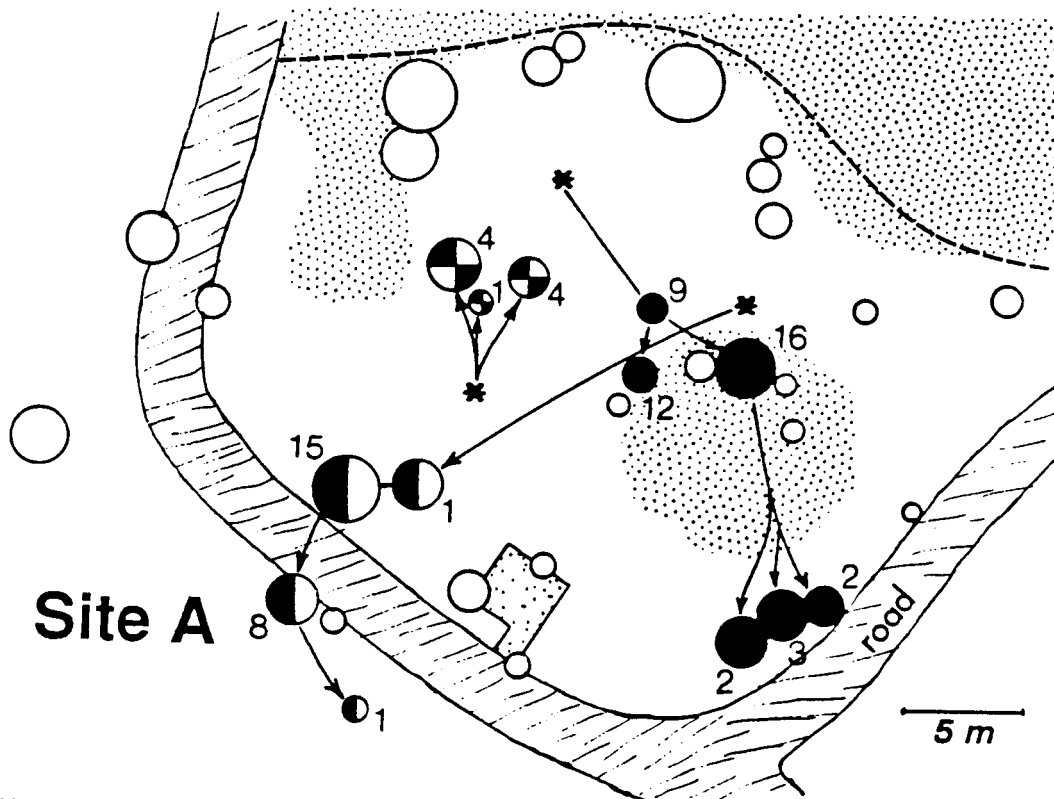
Howard 1983). In contrast, the relatively close spacing of mounds in polygyne populations has led several authors to suggest that colony reproduction in the polygyne form occurs by budding (Fletcher 1983, Greenberg et al. 1985, Porter et al. 1988), a mode of reproduction common among polygyne ants (Hölldobler & Wilson 1977). However, definitive evidence in this regard has been lacking. In this study, we sought direct evidence for budding in the polygyne form of *S. invicta* by introducing colonies containing marked queens to the field.

Materials and Methods

This study was conducted at two sites at the Brackenridge Field Laboratory of the University of Texas at Austin, Tex. The sites were largely open, grassy areas bordered by roads and shrubs (Fig. 1). In late March and early April 1987, the central areas of both sites were surveyed for *S. invicta*, the only species seen at both places. Site A had 77 mounds, of which 13 were at least 1 m in diameter; and site B had 22 mounds, of which seven were at least 1 m in diameter.

An effort was made to exterminate all ants in the central areas of the sites by treating the mounds individually with hot water (Tschinkel & Howard 1980). Hot-water treatment was used in this area to avoid harming the colonies to be introduced later. Each mound was thoroughly drenched with a forceful stream of scalding water from a hose attached to the building's hot water supply; the hose was inserted up to 1 m into the ground. To maximize effectiveness, the treatment was done at times of the day when the ants were concentrated at the tops of the mounds (e.g., warm sunny morn-

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ings). The areas were monitored for 3–4 wk after the start of the treatment, and any areas showing evidence of intact colonies (such as newly worked soil) were retreated until almost all pre-existing colonies were eliminated. To minimize reinvasion from outside areas, a zone (15–20 m wide) outside the central area was treated in early April with Logic (RO 13-5223, Maag Agrochemicals, Vero Beach, Fla.), a control bait containing an insect growth regulator.

Five mounds containing *S. invicta* were collected on the grounds of the Brackenridge Field Laboratory on 7 April 1987 from locations at least 0.25 km from either study site. These mounds were collected from sites at least 100 m from each other to avoid using closely connected mounds (i.e., mounds among which the ants may have been moving freely). Following collection, the ants were taken to the laboratory and separated from the soil by flooding (Jouvenaz et al. 1977). Each colony was housed individually in plastic trays (48 by 58 by 7 cm) equipped with 4–5 nests (14-cm diameter Petri dishes about half filled with damp plaster). The ants were maintained in the laboratory at $30 \pm 1^\circ\text{C}$ under a natural photoperiod (L:D) and fed ad lib. on an artificial diet derived from Banks et al. (1981), supplemented by frozen crickets, fresh mealworms, and pureed vegetables.

On 17 April 1987, all dealate (functional) and winged (nonfunctional virgin) queens were removed from the colonies by sieving (1.4 mm mesh). To estimate colony size, the workers and brood were weighed together to the nearest gram. The queens were chilled on ice and marked with fine wire (39 gage) by tying a ring around the petiole (Mirenda & Vinson 1979). All nestmate queens were marked with a color unique to their colony. In one colony, 20 alate virgin queens also were marked with a loop of colored wire; dissection and examination of three of these queens confirmed that they were uninseminated. To determine the durability of an ink mark under field conditions, 20 dealate queens from one colony were doubly marked with a uniquely colored wire and a spot of Tech Pen ink (Mark-Tex Corp., Englewood, N.J.) on the dorsum of the thorax. A sample of 9–15 dealate queens from each colony was dissected to estimate the proportion of uninseminated queens initially present in each colony. The composition of each colony is shown in Table 1.

After marking, the queens were reintroduced to their colonies and monitored for 2–3 d for mortality. Only 1 of the 367 marked queens died dur-

ing this time; the others appeared to behave normally. Following this observation period, the colonies were transferred to large plastic buckets approximately half-filled with damp soil taken from the study sites. The ants were allowed to dig into the soil and maintained there for a habituation period of 3–5 d. To facilitate introduction to the study sites, the bottoms had been cut off the buckets, the lids placed tightly on the tops, and the buckets inverted. The colonies were introduced to the study sites in holes (20–30 cm deep) by removing the lids from the bottom of the inverted buckets, allowing the ants to dig into the ground. Three colonies were introduced to Site A about 10 m apart on 22 April 1987 and two colonies to Site B about 15 m apart on 20 May (Fig. 1). Food was supplied for 7–10 d after introduction to the field. The sites were mowed every 2–4 wk for the duration of the study.

At the termination of the study, both sites were surveyed and mapped for ant mounds. At Site A, mounds were dug up on 22 and 24 September and a few more on 28 September, approximately 5 mo after introduction to the field. Site B was sampled on 30 September and 1 October 1987, about 4 mo following introduction. The ants were taken to the laboratory and separated from the soil by flooding. The ants from each mound were sieved to remove sexual forms, and the workers and brood were weighed together to the nearest gram. The dealate queens so obtained were carefully inspected for marks. All marked queens and a sample of their unmarked nestmates were dissected to determine their insemination status.

Voucher specimens have been deposited at the Brackenridge Field Laboratory and the Museum of Comparative Zoology, Harvard University, Cambridge, Mass.

Results

Fig. 1 shows the final location of mounds containing marked queens 4–5 mo after introduction to the study sites. Marked queens originating from the same study colony were found distributed among multiple nests in four of the five cases, clearly demonstrating that polygyne colonies of *S. invicta* reproduce by budding. One colony (#2, Site B) vanished except for one small nest with only two of the original 104 queens. The fate of this colony is uncertain; it may have been overrun by the other study colony, emigrated from the area,

Fig. 1. Fission and migration of five polygyne colonies of *S. invicta* over a 4–5 mo period (April–October 1987). Stars indicate introduction sites, arrows designate possible migration routes, solid and patterned circles represent the final locations of mounds with marked queens (the number of queens is indicated by each), open circles are mounds without marked queens. The area of each circle is proportional to total mound population (workers and brood). Shaded areas indicate trees or bushes. The central area of each site is enclosed by a dashed line and the asphalt road.

Table 1. Composition of polygyne colonies of *S. invicta* containing marked queens before and 5 mo after introduction to two study sites in the field

Site	Colony	Final no. mounds with marked queens	Original male size (g)	Original queens (marked)			Final queens						
				Final ^a size (g)	Marked		Unmarked						
					No.	Proportion inseminated	No.	Proportion inseminated	No. per colony $\bar{x} \pm SD$ (range)	No.	Proportion inseminated	No. per colony $\bar{x} \pm SD$ (range)	
													% Original queens re-covered
A	1	6	38	243	73	0.778	44	60.3	0.667	7.3 \pm 5.9 (2-16)	97	0.792	16.2 \pm 15.7 (1-38)
	2	3	75	104	29	0.400	9	31.0	0.714	3.0 \pm 1.7 (1-4)	84	0.696	28.0 \pm 27.6 (2-57)
	3	4	44	215	82	0.800	25	30.5	1.000	6.3 \pm 6.7 (1-15)	49	0.793	12.3 \pm 9.7 (1-11)
B	1	8	112	472	79	0.667	47	59.5	0.915	5.9 \pm 3.8 (1-11)	48	0.571	6.0 \pm 9.8 (1-30)
	2	1	98	5	104	0.600	2	2.0	—	2 (—)	0	—	— (—)
Total ^b		21	269	1,034	263		125	47.5			278		

^a Colony size is the combined live weight of workers and brood.^b Does not include colony B2.

or have been decimated by flooding or other natural causes. This colony was excluded from the following analysis. The absence of obvious signs of above-ground migration, such as columns of workers carrying brood or queens during casual observations of the study sites, suggests that movement of individuals occurs primarily underground.

Queens originating from the same nest were found distributed in different mounds considerable distances from each other (up to 50 m apart in the case of colony 1 at Site B). There was a large disparity in the number of marked queens originating from the same colony found in any one mound, with no apparent relationship between the number of marked queens in a mound and the distance moved from the point of introduction. A particularly surprising result was the lack of mixing of marked queens originating from different study colonies despite the long distances traveled and the fact that some colonies came to occupy areas originally inhabited by another colony. This suggests that there is no wholesale mixing of queens from different mounds which do not share some former connection, at least not during the summer. Thus it is of interest to know whether the rather free exchange of workers among some mounds in polygyne populations of this species (Bhatkar & Vinson 1987) also is limited to mounds having a common origin.

The proportion of marked queens that were inseminated increased in three of four colonies. This suggests differential survivorship among inseminated and uninseminated queens, although the sample sizes are rather small. Curiously, the proportion of newly added queens that were inseminated was about the same as the original marked queens.

One of the alate queens marked in colony 2 at Site A was retrieved; she had dealated, but dissection showed that she was uninseminated and lacked developed ovaries. One physogastric queen in colony 2 at Site A weighing 20.4 mg at the start was considerably more physogastric than any of her nestmate queens and was marked individually with two wires. She was collected again in a nest containing 28 other queens and was clearly the most physogastric.

The ink marks were surprisingly durable; 11 of the original 20 dealate queens marked with both ink and wire were retrieved. Of these, 10 had intact marks, whereas one had lost most of the mark but retained traces of ink in the thoracic sutures.

In addition to mounds containing marked queens, Site A had 22 mounds in which we found no marked queens in a total of 465 dealate queens collected. Similarly, Site B had five mounds containing a total of eight unmarked queens. Five of these mounds at Site A and two at Site B were located very close to mounds containing marked queens; they may have originated from study colonies but did not receive any of the original queens during colony division. Most of the other mounds lacking marked

queens probably migrated into the study sites from outside, although some may have remained from the original population.

The growth of the study colonies was substantial, increasing on the average almost four times, and in the case of colony 1 at Site A, increasing over six times. The final biomass of ants found at the two sites was remarkable; about 1.28 kg (about 2 g/m²) of ants was collected at Site A. Five small samples gave a mean of 1,217 workers/g of colony weight. This translates into some 1,560,000 workers at the site, or about 2,230 workers/m². This value is almost certainly well below the carrying capacity of the site, because 77 mounds were found and treated there at the start of the study, and only 30 mounds occurred at the end.

Discussion

Colony reproduction occurs by budding in the polygyne form of *S. invicta*. Moreover, it occurs at a fairly rapid rate; in an uninfested area, one mound can proliferate into as many as eight in about 4–5 mo. In addition, colony growth apparently can proceed at a remarkable pace during this period, increasing the total worker population by up to six times.

Once established, polygyne colonies of this dominant species can be expected to spread out as a continuous unicolonial population monopolizing the local habitat. Such local monopolization arising by budding accounts for the relatively close spacing of mounds of the polygyne form of *S. invicta* (Fletcher 1983, Lofgren & Williams 1984, Greenberg et al. 1985) and its mosaic distribution in the United States, where it tends to occur in discrete patches embedded within the surrounding monogyne populations (Fletcher 1983, Ross & Fletcher 1985, Ross et al. 1987). The expansion of one such local population is currently under study at Brackenridge Field Laboratory. Polygyne colonies of *S. invicta* have spread gradually across the station at a rate of about 35 m/yr (Porter et al. 1988). Furthermore, this expansion has resulted in nearly complete elimination of the native ant fauna of more than 45 species (S.D.P. & D. Savignano, unpublished data). Similar invasions have been observed in several other polygyne ants, most notably the cosmopolitan pest species *Iridomyrmex humilis* (Mayr) and *Pheidole megacephala* (F.) (Hölldobler & Wilson 1977).

The differing modes of reproduction of the monogyne and polygyne forms of *S. invicta* resemble the occurrence of different reproductive strategies among pairs or groups of closely related monogyne and polygyne species of ants (Wilson 1971, Hölldobler & Wilson 1977, Brian 1983). Comparative data suggest that polygyne forms evolve from monogyne forms in response to ecological factors such as habitat specialization (Hölldobler & Wilson 1977, Pamilo & Rosengren 1984, Fletcher & Ross 1985). The presence of multiple queens and the

related occurrence of large diffuse colonies and budding as a means of colony reproduction appear to permit polygyne forms to occupy habitats, often marginal, where related monogyne forms are less able to persist. Whereas little is known regarding the origin of polygyny in *S. invicta*, its occurrence in the United States does not appear to be related to habitat specialization, because the polygyne form does not occupy habitats different from those of the monogyne form (Greenberg et al. 1985, Ross & Fletcher 1985, unpublished data). Thus the selective forces, if any, promoting and maintaining polygyny in this species remain to be identified.

Although these results emphasize aspects of reproduction unique to the polygyne form of *S. invicta*, it is important to note that some features of its reproductive behavior also are found in the monogyne form. Monogyne colonies typically possess a single mound, but many colonies change the location of the mound frequently and, on occasion, appear to occupy one or more satellite mounds (Lofgren et al. 1975, Hays et al. 1982). It seems likely that such behavior could easily lead to budding when multiple queens are present.

Another important similarity between the monogyne and polygyne forms of this species is that polygyne colonies do have mating flights, although the newly mated queens they produce have fewer body reserves and appear to be far less capable of succeeding at independent colony founding than their monogyne counterparts (Porter et al. 1988). Thus, there exists the possibility that polygyne colonies of *S. invicta* employ a mixed mode of colony reproduction involving both budding and independent foundation, as apparently occurs in the polygyne ant *Lastus sakagami* Yamauchi & Haya-shida (Yamauchi et al. 1981). Important unanswered questions concerning the possibility of independent colony founding by polygyne colonies of *S. invicta* are whether and to what extent newly mated queens found colonies independently and, if so, whether the resulting colonies are monogyne or polygyne.

The source of the unmarked queens found cohabiting with the marked queens at the end of the study remains unknown. Perhaps they were survivors of the initial extermination effort and joined ranks with the study colonies later. This seems unlikely because of the thoroughness of our treatment, the large number of unmarked queens, and the apparent lack of movement of queens among existing mounds. The more likely possibilities concerning the source of additional queens in polygyne colonies of *S. invicta*, such as the unmarked queens found in the present study, comes from knowledge of the source of functional queens in other polygyne ants. Additional queens may originate from intranidal matings (e.g., in *Monomorium pharaonis* (L.) [Wilson 1971] and *Iridomyrmex humilis* (Mayr) [Markin 1970, Passera et al. in press], adoption of newly mated queens following nuptial flights (e.g., in *Formica ulkei* Emery [Scherba 1958], *For-*

mica opaciventris Emery [Scherba 1961], and the microgyne form of *Myrmica ruginodis* Nylander [Brian 1983, Kasugai et al. 1983]), or adoption of post-claustral founding queens (e.g., in *Pseudomyrmex venefica* Wheeler [Janzen 1973]). Recent data from Glancey and Lofgren (in press) suggest that adoption of newly mated queens is the most likely source of additional queens in polygyne *S. invicta*.

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